

Fuel stores, fuel accumulation, and the decision to depart from a migration stopover site

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Birds usually migrate by alternating flight bouts and stopovers for refueling. The decision when to leave a stopover place is of paramount importance for the success of migration. Despite its importance, little is known about which factors influence the departure decision. Using capture–recapture data of passerines from 3 stopover sites, we investigate by capture–recapture models whether this decision is dependent on actual fuel stores and fuel deposition rates. Individuals that accumulated fuel stores at medium rates departed later than individuals that either lost fuel stores during their stopover or able to increase their fuel stores quickly. This pattern was consistent among all sites. The departure decision was not dependent on actual fuel stores at 2 stopover sites. At the site facing an ecological barrier, emigration probability increased with increasing fuel stores, indicating that birds wait until they reach a threshold of fuel stores before departing. There was a positive correlation between departure fuel load and fuel deposition rate at all sites, which is in accordance with the time-minimizing hypothesis. These results suggest that the decision to depart from a stopover site is based on rather simple behavioral rules: birds that lose fuel stores or that increase fuel stores at a high rate would leave a site quickly, whereas birds increasing fuel stores at intermediate rates would stay for a longer time. The departure decision is shaped also by the position of the stopover site in relation to the next one and may be affected further by environmental factors. *Key words:* capture–recapture model, fuel deposition rate, passerine, take-off probability, trans-Saharan migrant. [*Behav Ecol* 19:657–666 (2008)]

Migrating birds usually divide their journey from the breeding to the wintering grounds and back into alternating phases of flight bouts and stopovers. At the stopover sites, the energy needed for flight is accumulated and the migrants have to decide when to depart for the next flight bout. This decision determines the time birds spend at stopover sites and the amount of fuel that can be used during the next flight bout. The resulting overall speed of migration is mainly the consequence of these stopover decisions. It determines arrival time at the breeding or wintering grounds and at intermittent stopover sites. Because survival and reproduction depend on the seasonally variable conditions at these locations (e.g., Ricklefs 1974; Möller 1994; Cristol 1995; Farmer and Wiens 1999), migration speed should be optimized to maximize fitness. Clearly, the decision when to leave a stopover site is central not only for successful migration but also has important fitness consequences.

Factors potentially involved in the departure decision are either intrinsic, such as actual fuel stores, fuel deposition rate (change in fuel stores over time), and the endogenous time program (time pressure), or environmental such as weather conditions at ground and aloft or predation risk (reviewed in Jenni and Schaub 2003). Despite its fundamental importance, relatively little is known about which factors govern the decision to leave a stopover site (Berthold 1996; Jenni and Schaub 2003). Moreover, regarding intrinsic factors, findings of the few available field studies on how actual fuel stores and fuel deposition rate affect the decision to depart from a stopover site are controversial (reviewed in Jenni and Schaub 2003).

Experiments suggest that stopover duration is very short if fuel deposition rate is low or negative (Biebach 1985; Gwinner et al. 1985; Yong and Moore 1993). It remains unclear how stopover duration is regulated when fuel deposition rate is positive and whether it is regulated in the same way at all stopover sites along the migration route irrespective of the distance to the next stopover site. From some studies, there is evidence that lean birds stay longer than fat birds before crossing an ecological barrier or during stopovers in a desert oasis (e.g., Bairlein 1985a, 1987; Biebach et al. 1986), but not from another (Salewski and Schaub 2007). When birds migrate over areas with many stopover sites, no clear pattern of the regulation of stopover duration appears (reviewed in Jenni and Schaub 2003).

The main reason for the lack of knowledge about whether migrating birds consider actual energy stores or fuel deposition rate for their decision to leave a stopover site is the difficulty to determine departure time and, even more so, the amount of fuel at departure in the field. A possibility to overcome these problems is to combine the estimation of emigration probability from capture–recapture data (Lebreton et al. 1992) with estimates of fuel stores and fuel deposition rates of recaptured birds (Schaub and Jenni 2000; Schaub 2006). Using these methods, the main aim of this study is to test whether and how fuel deposition rate and actual fuel stores are related to departure of passerine trans-Saharan migrants from 3 different stopover sites and whether the patterns are consistent among stopover sites.

The results are used to assess 3 different hypotheses put forward to explain which intrinsic factors birds use to decide when to leave a stopover site.

- (a) Optimal bird migration theory predicts that birds should adjust their departure fuel load, hence stopover duration, to their fuel deposition rate if they are constrained by time and, thus, aim at minimizing time spent on migration (Alerstam and Lindström 1990;

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Alerstam and Hedenström 1998). Under this hypothesis, a positive correlation between departure fuel load and fuel deposition rate is expected. The alternative, that is, to minimize energy used for migration, predicts departure fuel load to be independent of fuel deposition rate but is less likely because long-distance migrants are always to some extent constrained by time, due to their tight annual schedule.

- (b) Modeling the success of migration in a heterogeneous environment demonstrated that birds using a rule of thumb (stay 10 days at each stopover site, provided that fuel deposition rate is positive) are only marginally less successful than birds behaving according to optimal migration theory under time constraint (Erni et al. 2002). Under this hypothesis, we would expect departure to be independent of fuel deposition rate and fuel load.
- (c) For birds that have to cross a great distance without the possibility to refuel, the strategy (b) would not be of great help. Instead, they should aim to reach a threshold departure fuel load more than sufficient to cross the barrier (Weber et al. 1998). Thus, we would expect departure to depend on departure fuel load irrespective of fuel deposition rate.

These 3 hypotheses hold for stopover sites where birds gain energy stores. In case birds lose stores, they should leave the stopover site as soon as possible and seek a better site (Jenni and Schaub 2003).

MATERIALS AND METHODS

Sites and data sampling

Migrant passerine species were caught at 54 sites throughout Europe and North Africa during 3 autumn migration periods (1994–1996) in a collaboration of bird-ringing stations within a European Science Foundation Network (Bairlein 1995, 1997). At sites where a migrating species also breeds, the capture sample consists of local birds not yet on migration and of individuals on passage, which usually cannot be distinguished from each other. For robust tests of our hypotheses, we needed data sets that consisted only of birds on passage, which produced many recaptures. Therefore, we selected only species with at least 80 recaptures from sites where the species does not breed in the area. We could use 3 data sets: 1) willow warblers *Phylloscopus trochilus* from the small (2 km²) Wadden Sea island Oldeog (northern Germany, 53.8°N, 8.0°E); the island is within the breeding range of the willow warbler, but the species does not breed there. 2) Pied flycatchers *Ficedula hypoleuca* in the bushy area of the National Park Coto de Doñana (southern Spain, 37.2°N, 6.5°W); the southern part of the Iberian peninsula is outside the breeding range of this species. 3) Reed warblers *Acrocephalus scirpaceus* at Moulouya (northern Morocco, 34.1°N, 2.5°E), a site with riparian *Tamarix* bushes; there are few breeding reed warblers in Morocco, but none at the study site. All 3 species breed in Europe and winter south of the Sahara desert (Cramp 1992, 1993).

Data were collected in a standardized way (Bairlein 1995), that is, the nets were opened daily from dawn to dusk during the migration season and checked every hour. Every bird captured was ringed individually, and the following data were recorded: age according to Jenni and Winkler (1994), body mass (to the nearest 0.1 g), length of primary feather 8 (0.5 mm, according to Jenni and Winkler 1989), and date and time of capture (to the nearest hour). Apart from the length of primary 8 (P8), the same measurements were taken from birds that were recaptured at the same site. We considered only birds that were captured during the main migration period for the species at that site (Table 1).

Statistical analyses

Our goal was to test whether and how emigration probability depended on actual fuel stores and on fuel deposition rate. Cormack–Jolly–Seber (CJS) models allow to separately estimate apparent survival probability (ϕ_i : the probability that a marked bird survived and did not emigrate permanently from the study site between capture occasion i to the next one $i + 1$) and recapture probability (P_i : the probability that a marked bird that is alive and present at the study site at i is captured at time i) from capture–recapture data (Lebreton et al. 1992). During the rather short period of stopover in passerines (Schaub and Jenni 2001a), it can safely be assumed that true survival is nearly 1. Hence $1 - \phi_i$ is an estimate of the probability that a bird has left the study site between i and $i + 1$ (Schaub and Jenni 2001a; Schaub et al. 2001). This emigration probability ($\varepsilon_i = 1 - \phi_i$) can be modeled as a function of time-invariant individual covariates. For the interpretation, it is important to note that emigration is defined as the emigration from the capture place; thus, emigrated birds could either have started for a next migratory flight (i.e., have departed) or just have moved to another habitat patch that is not covered by nets. However, passerines often move within a stopover area only a short time after arrival (Chernetsov and Titov 2000; Bächler and Schaub 2007). It therefore appears that fitting capture–recapture models which take account of transients, as we will do, is efficient to estimate departure (Bächler and Schaub 2007).

Fuel deposition rate was estimated as the change in body mass between first and last capture divided by the time elapsed between these captures. It is an integrative estimate of body mass change over a longer period of time and was therefore regarded as a time-invariant covariate. In contrast, fuel stores of an individual differ at each capture event. If the decision to leave the stopover site would depend on fuel stores, emigration probability would change as fuel stores change. Therefore, fuel stores at first capture is not an appropriate covariate to explain emigration probability. Rather, the emigration probability of a bird should change as a function of its current fuel stores. This cannot be modeled with the standard CJS model but requires a multistate capture–recapture model (Nichols et al. 1992). In this model, birds are allowed to change their fuel stores during stopover, and the emigration probability for a bird with its actual fuel stores can be estimated. Because

Table 1

Location of the sites, species studied, operating years, main migration period considered, total number of birds caught (n), number of birds recaptured at least once (u), and number of birds recaptured at least twice (t)

Site	Species	Location	Operating years	Seasonal sampling periods	n	u	t
Oldeog (D)	Willow warbler	Island	1994–1996	1 August–25 September	3797	323	87
Coto de Doñana (ES)	Pied flycatcher	Mainland	1994, 1995	9 September–14 October	897	112	46
Oued Moulouya (MO)	Reed warbler	Mainland	1994, 1996	8 September–24 October	394	84	30

body mass and its rate of change (fuel deposition rate) are statistically not independent, it is impossible to estimate their correlation from the available data. This makes it difficult to find out whether fuel stores or fuel deposition rate is the more important determinant of emigration probability. A capture–recapture model in which the birds are assigned to a class of fuel deposition rate and to a class of fuel stores at initial capture helps to overcome this difficulty but does not account for changes in fuel stores class during stopover.

By consequence, we performed 2 analyses per site. First, we tested the effect of actual fuel stores on emigration probability using a multistate capture–recapture model with 3 fuel store states. The second analysis explored the dependence of emigration probability on both fuel deposition rate and fuel stores at initial capture with a 1-state capture–recapture (i.e. CJS) model where fuel deposition rate and fuel stores were continuous individual covariates. In all analyses, we did not include possible variation between years or days within years. This would have required a huge amount of data.

Emigration probability and actual fuel stores

We regressed body mass of all birds per site against time of day of capture (time) and length of P8. We used the estimated regression coefficients (willow warbler: time = 0.005 [standard error {SE} = 0.003], P8 = 0.201 [SE = 0.005], $n = 3531$; pied

the probability that a marked bird that has survived locally from time i to $i + 1$ in state m changes to state n shortly before $i + 1$). In order to account for and to estimate the probability that a newly caught individual is a transient for each of the 3 fuel store states and to allow changes in fuel store states of the nontransients during stopover, we considered a model with 7 different states. Depending on their index of fuel stores at first capture, all birds captured for the first time are in 1 of 3 states “initially low” (state 1), “initially medium” (2), or “initially high” (3). During the next recapture period, all birds move either to 1 of the 3 states “nontransient low” (4), “nontransient medium” (5), or “nontransient high” (6) when they are nontransient or to the state “transient” (7) when they are transients. Transient birds emigrate immediately after first capture and thus have an emigration probability of 1. Only birds that are in one of the nontransient state can be recaptured. The movement probabilities from one of the initial states to the nontransient state are the state-specific probabilities that the birds are nontransient ($1 - \tau$). Subsequent movements between nontransient fuel store states are the daily probabilities of fuel store changes (ψ). Changes from a nontransient state to an initial state as well as changes between initial states are not possible. This model can be written with the transition matrix (states of departure in rows and states of arrival in columns) and 2 vectors with state-specific emigration and recapture probabilities:

$$\begin{bmatrix} 0 & 0 & 0 & 1 - \tau^l & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 1 - \tau^m & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & 1 - \tau^h & 0 \\ 0 & 0 & 0 & 1 - \psi^{lm} - \psi^{lh} & \psi^{lm} & \psi^{lh} & 0 \\ 0 & 0 & 0 & \psi^{ml} & 1 - \psi^{ml} - \psi^{mh} & \psi^{mh} & 0 \\ 0 & 0 & 0 & \psi^{hl} & \psi^{hm} & 1 - \psi^{hl} - \psi^{hm} & 0 \\ 0 & 0 & 0 & 0 & 0 & 0 & 1 \end{bmatrix}, \begin{bmatrix} \tau^l \\ \tau^m \\ \tau^h \\ \varepsilon^l \\ \varepsilon^m \\ \varepsilon^h \\ 1 \end{bmatrix}, \begin{bmatrix} 0 \\ 0 \\ 0 \\ p^l \\ p^m \\ p^h \\ 0 \end{bmatrix}. \quad (1)$$

flycatcher: time = 0.115 [SE = 0.012], P8 = 0.110 [SE = 0.023], $n = 879$; reed warbler: time = 0.126 [SE = 0.028], P8 = 0.185 [SE = 0.052], $n = 394$) to calculate for each bird and each capture event an adjusted body mass (adjusted to 12 h and to 50.5 mm [willow warbler], 60.5 mm [pied flycatcher], and 50 mm [reed warbler] of P8). From these measures, we subtracted lean body mass (willow warbler 7.0 g, pied flycatcher 10.9 g, reed warbler 10.3 g; Schaub and Jenni 2000) and divided the resulting value by lean body mass. The index of fuel stores at each capture was considered to be “low” when it was < 0.15 , “medium” when between 0.15 and 0.35, and “high” when > 0.35 . The individual capture histories used for the analyses contained zeros at days when the corresponding bird was not captured and codes for the fuel store states at days when it was captured.

We intended to model emigration of nontransient birds (in the sense that their emigration probability just after initial capture is not 1) in relation to actual fuel stores using a multistate capture–recapture model. Transient models have been developed by Pradel et al. (1997) for 1-state models (see also Schaub et al. 2004)—here we use an approach for multistate models (Bächler and Schaub 2007).

Compared with the 1-state capture–recapture models, multistate capture–recapture models are parameterized with state-specific emigration and recapture probabilities and with an additional parameter to allow for changes between states (ψ_i^{mn} ,

Parameter superscripts indicate state or changes between fuel store states, whereby l refers to low, m to medium, and h to high. The state-specific emigration probabilities of the 3 initial states are constrained to be zero to ensure that nontransients do not emigrate during the interval following initial capture. This is different from the usual transient models by Pradel et al. (1997), in which nontransient animals are allowed to die (i.e., emigrate) during the interval following initial capture (Schaub et al. 2004). Our model can easily be fitted with the software MARK (White and Burnham 1999). However, all first captures in the original capture histories with the 3 states low, medium, and high have to be recoded to the new states initially low, initially medium, and initially high.

To explore the importance of actual body mass on emigration probability and to correct for the occurrence of transients, we considered models with and without state-specific estimates (ε^n , ε , τ^n , and τ). We did not impose constraints in the change parameters between the nontransient states (ψ^{mn}), that is, 6 probabilities were estimated. In order to get rough estimates in these parameters, we did not consider temporal variation. The recapture probabilities were thought to be time dependent but the same in all states (P_t), time dependent and different by a constant (indicated by +) between the states (P_{t+}^m), the same in all states (P), and state specific (P^m). In total, we considered 16 models, and we used the modified Akaike

Table 2
GOF test results obtained by U-CARE of the CJS model for data sets containing all captures

Test component	CJS model					Transient model		
	χ^2	df	<i>P</i>	<i>z</i>	<i>P</i> (1 sided)	χ^2	df	<i>P</i>
<i>Oldeoog</i>								
3.SR	74.24	19	<0.001	6.38	<0.001			
Total	100.00	66	0.004	—	—	25.76	47	1.00
<i>Coto de Doñana</i>								
3.SR	90.17	29	<0.001	7.45	<0.001			
Total	151.64	109	0.004	—	—	61.47	90	0.99
<i>Moulouya</i>								
3.SR	19.00	37	0.99	2.27	0.02			
Total	50.77	133	1.00	—	—	31.77	96	1.00

We show the global test results, as well as the subtest 3.SR. 3.SR tests whether the probability to recapture birds that were captured at *t* depends on whether they have been caught already before *t*. The most likely reason for a significant test result of 3.SR is the occurrence of transients. We show the results of directional tests in 3.SR, which test whether the directions of deviations were consistent. The GOF test of the model that accounts for transients is indicated as well. df, degrees of freedom.

information criterion (AIC_c) for model selection, which accounts for small sample size (Burnham and Anderson 1998). The model with the smallest AIC_c value was accepted as the most parsimonious model and was used for making inferences.

Recently, a goodness-of-fit test (GOF) for multistate capture–recapture models has been proposed (Pradel et al. 2003), but not for the multistate transient model. The best we could do was to test the GOF of the corresponding 1-state capture–recapture model, which does not account for possible differences of emigration and transient probabilities due to actual fuel stores with U-CARE (Choquet et al. 2001). The GOF results showed that at Oldeoog and the Coto de Doñana, a significant proportion of transients prevailed (Table 2), as indicated by the significant test component 3.SR and the positive *z* value. The GOF of the CJS model of the Moulouya data set was not significant; however, the significant directional test indicated that there were at least some transients (Table 2). The GOF of the models that account for transients were acceptable in all 3 data sets, and we assume that the more general multistate transient model would have an acceptable fit as well.

Relating emigration probability to fuel deposition rate and fuel stores at capture

We regressed body mass of all birds caught for the first time at a site against capture time, its square, the age of the bird, and the interaction of age with time and with time squared. In the reed warbler and in the pied flycatcher data sets, only the variable time revealed statistical significance but in the willow warbler (*n* = 3747) none. Using the regression coefficients of time (reed warbler 0.121 g h^{−1} [SE = 0.028], *n* = 392; pied flycatcher 0.115 g h^{−1} [SE = 0.012] *n* = 884), we adjusted each individual body mass to 12 h. For the willow warbler, the unadjusted body mass was used. We calculated individual fuel deposition rates as the quotient of the adjusted body mass difference and the number of days between first and last capture. We divided the individual fuel deposition rate by lean body mass of the species (values as above). Fuel stores at capture were calculated as the quotient of adjusted body mass at second capture minus lean body mass and lean body mass.

Fuel deposition rates were only available for birds caught at least on 2 different days, but in capture–recapture analyses, all captured animals have to be included. To overcome this prob-

lem, we followed an approach proposed by Pradel et al. (1997), originally developed for the estimation of survival rates of animals that are nontransients. The first capture event of all birds is deleted in the capture history data file, resulting in a file that contains only birds that were originally caught at least twice. These analyses provide estimates of emigration probabilities of nontransients.

We analyzed the capture histories of the reduced data sets with program MARK (White and Burnham 1999) and modeled the emigration and the recapture rates as functions of the individual fuel deposition rates *f* and the individual fuel stores *m* (Skalski et al. 1993). We used the logit link in all models, and thus, as an example, the emigration probability ε_i for bird *i* with the fuel deposition rate *f_i* and fuel stores *m_i* under model [$\varepsilon(f + f^2 + m)$, $P(\cdot)$] is estimated as follows:

$$\varepsilon_i = 1 - \frac{\exp(\beta_0 + \beta_1 f_i + \beta_2 f_i^2 + \beta_3 m_i)}{1 + \exp(\beta_0 + \beta_1 f_i + \beta_2 f_i^2 + \beta_3 m_i)}. \quad (2)$$

Program MARK gives estimates and precision of the β terms. Differentially parameterized models had subsequently different number of β terms.

A priori considerations let us presume that emigration rates are nonlinear functions of either fueling rates or fuel load. For example, high and low fuel deposition rates might have a similar effect on the emigration rates. Birds losing body mass might leave the site after a short time because it is not rewarding, whereas birds that increase body mass might leave the site soon because they have attained a suitable amount of fuel in a short time. Alternatively, emigration probability may be a linear function of fuel deposition rate and/or fuel stores. In order to detect and to test for significance for a variety of possible patterns, we modeled the emigration probability as functions of order 2 of individual fuel deposition rate and fuel stores. We also included the interaction between the 2 main effects because the effect of fuel deposition rate on the emigration probability might depend on the fuel stores. For the recapture probability, the same relationships seem possible. Thus, the most complicated model from which we started model selection was symbolized as [$\varepsilon(m + m^2 + f + f^2 + mf)$, $P(m + m^2 + f + f^2 + mf)$]. We followed the model selection strategy proposed by Lebreton et al. (1992). First, we reduced the structure of the recapture probability by fitting model with subsequently reduced complexity. Once the best structure for the recapture probability

Table 3

Modeling emigration probabilities (ϵ), proportion of transients (τ), and recapture probabilities (P) at the 3 sites as a function of actual fuel stores (m) and time (t)

Model	Oldeog				Coto de Doñana				Moulouya			
	Deviance	n.p.	ΔAIC_c	Weight	Deviance	n.p.	ΔAIC_c	Weight	Deviance	n.p.	ΔAIC_c	Weight
$\epsilon^m, \tau^m, \psi, P_t^m$	771.9	48	6.32	0.01	1288.9	49	12.52	0.00	952.3	60	55.49	0.00
$\epsilon^m, \tau^m, \psi, P_t$	773.2	46	3.49	0.05	1295.6	47	14.86	0.00	953.0	58	51.00	0.00
$\epsilon^m, \tau^m, \psi, P^m$	907.3	15	74.46	0.00	1354.6	15	6.01	0.04	1007.8	15	5.91	0.03
$\epsilon^m, \tau^m, \psi, P$	916.0	13	79.20	0.00	1391.1	13	38.38	0.00	1009.6	13	3.45	0.11
$\epsilon^m, \tau, \psi, P_t^m$	774.5	46	4.77	0.03	1289.8	47	9.12	0.01	952.6	58	50.62	0.00
$\epsilon^m, \tau, \psi, P_t$	777.3	44	3.50	0.05	1295.7	45	10.64	0.00	954.1	56	47.08	0.00
$\epsilon^m, \tau, \psi, P^m$	907.5	13	70.69	0.00	1355.9	13	3.12	0.15	1007.8	13	1.68	0.26
$\epsilon^m, \tau, \psi, P$	918.1	11	77.23	0.00	1391.4	11	34.51	0.00	1010.3	11	0.00	0.59
$\epsilon, \tau^m, \psi, P_t^m$	772.3	46	2.54	0.09	1290.8	47	10.05	0.00	961.3	58	59.39	0.00
$\epsilon, \tau^m, \psi, P_t$	773.8	44	0.00	0.30	1296.3	45	11.26	0.00	964.6	56	57.59	0.00
$\epsilon, \tau^m, \psi, P^m$	907.5	13	70.62	0.00	1390.6	13	37.81	0.00	1016.3	13	10.11	0.00
$\epsilon, \tau^m, \psi, P$	915.3	11	74.47	0.00	1392.0	11	35.18	0.00	1021.5	11	11.11	0.00
$\epsilon, \tau, \psi, P_t^m$	774.8	44	0.96	0.19	1291.2	45	6.13	0.03	965.1	56	58.11	0.00
$\epsilon, \tau, \psi, P_t$	778.2	42	0.21	0.27	1297.2	43	7.76	0.02	966.7	54	54.67	0.00
$\epsilon, \tau, \psi, P^m$	913.1	11	76.31	0.00	1356.9	11	0.00	0.74	1020.8	11	10.49	0.00
ϵ, τ, ψ, P	921.9	9	77.00	0.00	1392.3	9	31.39	0.00	1023.8	9	9.30	0.01

Parameter superscripts denote state dependence and parameter subscripts time dependence. The transition probability between fuel store states (ψ) was not modeled. Deviance, model deviance; n.p., number of estimated parameters; ΔAIC_c , difference in small sample size adjusted, computed as $\Delta AIC_{ci} = AIC_{ci} - AIC_{cmin}$; weight, the Akaike weight. The most parsimonious model for each site is highlighted in bold.

was found, it was held unchanged and different models of the survival part with varying complexity were fitted. For each site, the same models were tested. We used the AIC_c to rank the models according to their importance.

At present, there is no established method for testing the GOF of capture–recapture models with individual covariates. We therefore divided all birds into 4 groups according to their individual fuel deposition rate (smaller than zero and larger than zero) and the fuel stores (below mean and above mean) and assessed the GOF of the model [$\phi_{g \times b} P_{g \times l}$] with program U-CARE (Choquet et al. 2001). These GOF tests were insignificant in all data sets (willow warbler: $\chi^2_{128} = 20.9$, $P = 1.00$; pied flycatcher: $\chi^2_{74} = 23.6$, $P = 0.99$; reed warbler: $\chi^2_{40} = 8.2$, $P = 1.00$). Thus, there was no indication of significant heterogeneity in the data, and we concluded that the model with individual covariates is likely to fit the data as well.

Estimating departure fuel load

We calculated departure fuel load of nontransient birds based on the estimated relationship between individual fuel deposition rate, fuel stores, and emigration probability and under the assumption that fuel deposition rate is constant over this time period. The duration of stay of a bird i with fuel deposition rate f_i and fuel stores m_i from the first recapture until departure is calculated as $S_i = -1/\ln \epsilon(f_i, m_i)$, where $\epsilon(f_i, m_i)$ is the estimated emigration probability for bird i using the most parsimonious model for the corresponding site. Departure fuel load is then calculated as $D_i = m_i + S_i \times f_i$. To test the time-minimization hypothesis, we computed the correlation between D_i and f_i . For this analysis, only birds that increased body mass (i.e., $f_i > 0$) were considered.

RESULTS

Emigration probability and actual energy reserves

At Moulouya, the emigration probability of nontransient reed warblers was dependent on the actual fuel stores (Table 3, Figure 1). Nontransients with high fuel stores had a much higher daily probability to leave Moulouya than conspecifics

with medium or low energy stores. In contrast, the departure decision of willow warblers from Oldeog and of pied flycatchers from the Coto de Doñana was not dependent on fuel stores.

At the 2 mainland sites Moulouya and Coto de Doñana, the probability that newly caught individuals were transients was independent of the fuel stores (Table 3). On the island Oldeog, the model-averaged transient probability was slightly higher in heavy birds (0.25, SE: 0.09) than in medium (0.19, SE: 0.05) and light birds (0.17, SE: 0.06).

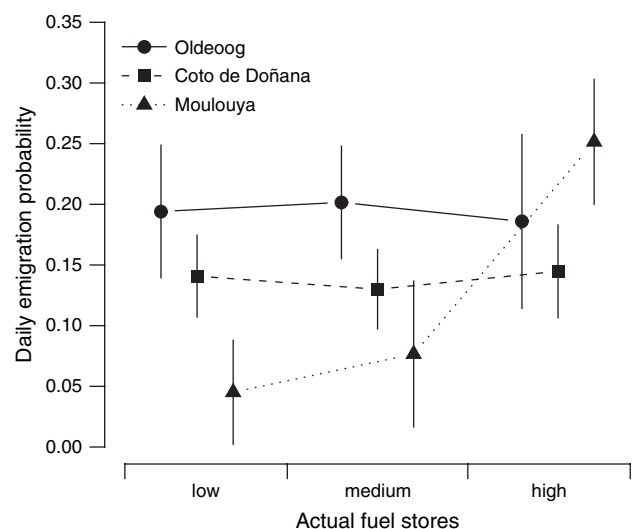


Figure 1

Model-averaged daily emigration probabilities (all models in Table 3 considered) as a function of the actual fuel store index at the 3 sites. The categories refer to birds with low fuel reserves (<0.15 of lean body mass), medium fuel reserves (between 0.15 and 0.35 of lean body mass), and high fuel reserves (>0.35 of lean body mass). Vertical lines show the model-averaged SEs of the point estimates.

Table 4

Modeling recapture probabilities (P) at the 3 sites as a function of individual fuel store index at second capture (m) and fuel deposition rates (f)

Recapture model	Oldeog				Coto de Doñana				Moulouya			
	Deviance	n.p.	ΔAIC_c	Weight	Deviance	n.p.	ΔAIC_c	Weight	Deviance	n.p.	ΔAIC_c	Weight
$m + m^2 + f + f^2 + mf$	829.9	12	0.90	0.13	546.8	12	0.69	0.11	310.7	12	7.03	0.01
$m + m^2 + f + f^2$	835.8	11	4.72	0.02	550.3	11	1.93	0.06	310.8	11	4.68	0.03
$m + m^2 + f + mf$	836.7	11	5.65	0.01	550.8	11	2.41	0.05	310.7	11	4.57	0.03
$m + f + f^2 + mf$	831.1	11	0.00	0.20	548.4	11	0.00	0.16	311.2	11	5.06	0.02
$m + m^2 + f$	837.9	10	4.69	0.02	552.5	10	1.80	0.06	310.8	10	2.27	0.09
$m + f + f^2$	836.0	10	2.83	0.05	551.4	10	0.71	0.11	311.4	10	2.83	0.06
$m + f + mf$	837.3	10	4.12	0.03	551.9	10	1.26	0.08	311.2	10	2.65	0.07
$m + m^2$	837.9	9	2.59	0.05	556.3	9	3.40	0.03	316.9	9	6.02	0.01
$f + f^2$	837.9	9	2.56	0.06	556.2	9	3.30	0.03	313.2	9	2.33	0.08
$m + f$	838.2	9	2.89	0.05	553.3	9	0.40	0.13	311.4	9	0.47	0.21
m	838.2	8	0.84	0.13	556.3	8	1.25	0.08	317.0	8	3.81	0.04
f	839.5	8	2.17	0.07	557.3	8	2.23	0.05	313.2	8	0.00	0.27
.	839.6	7	0.11	0.19	559.7	7	2.42	0.05	317.8	7	2.28	0.08

The emigration model is always kept at the most complex structure $\varepsilon(m+m^2+f+f^2+mf)$. For heading explanations, see Table 3. The most parsimonious model for each site is highlighted in bold. n.p., number of estimated parameters.

Emigration probability and fuel deposition rate

At all 3 sites, body mass increased on average during stopover (Oldeog: 0.43% of lean body mass day⁻¹ [standard deviation {SD} 6.15%], $n = 323$; Coto de Doñana: 1.37% day⁻¹ [SD 4.02%], $n = 112$; Moulouya: 1.83% day⁻¹ [SD 2.94%], $n = 84$).

The emigration probability of nontransients clearly depended on individual fuel deposition rate at all 3 sites (Tables 4 and 5). The daily emigration probability was highest for birds with negative and highly positive fueling rates, and it was lowest for birds with intermediate fueling rates (Figure 2). This u-shaped pattern was similar at all 3 sites. Thus, birds that lost body mass or that were able to increase body mass at a high rate spent a significantly shorter time at the stopover sites after initial capture compared with birds with intermediate fueling rates. Consistent with the previous analysis, fuel stores at capture only affected emigration probability at Moulouya, but not at the other sites (Table 5). At Moulouya, emigration probability increased with increasing fuel stores (Figure 2).

Departure fuel load

Departure fuel load increased significantly with positive fuel deposition rates at all 3 sites (Figure 3). Because departure fuel load is calculated from fuel deposition rate, the 2 variables are not independent and a positive correlation between the 2 can be expected also if there is no biological association between them (Brett 2004). If so, the same mathematical dependence must hold also for negative fuel deposition rates. The correlation coefficients between departure fuel load and fuel deposition rates were smaller and apart from Oldeog not significantly different from zero for birds with negative fuel deposition rates (Oldeog: $r_{151} = 0.17$, $P = 0.03$; Coto de Doñana: $r_{30} = 0.31$, $P = 0.09$; Moulouya: $r_{16} = 0.14$, $P = 0.57$). Therefore, there is evidence that the positive correlations between departure fuel load and fuel deposition rates were not only due to the mathematical dependence but also reflect (partly) true positive correlation.

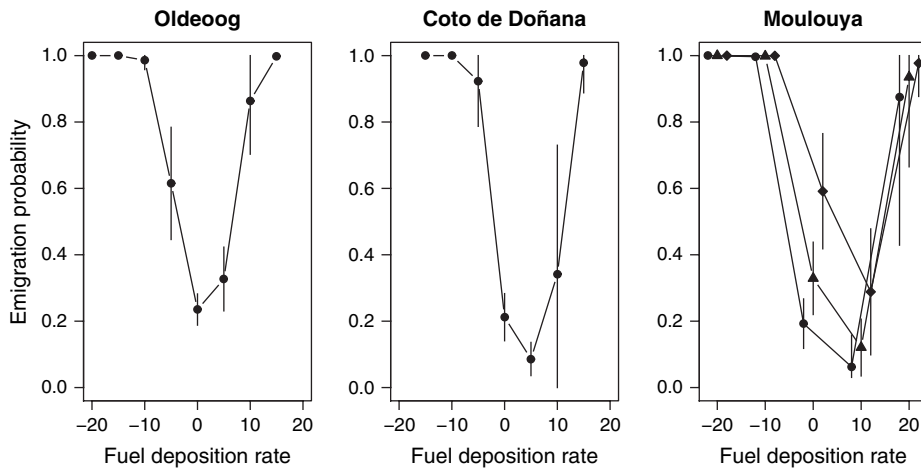
A significant negative correlation between initial fuel load and fuel gain from initial capture until departure was apparent

Table 5

Modeling emigration (ϵ) at the 3 sites as a function of individual fuel store index at second capture (m) and fuel deposition rates (f)

Emigration model	Oldeog				Coto de Doñana				Moulouya			
	Deviance	n.p.	ΔAIC_c	Weight	Deviance	n.p.	ΔAIC_c	Weight	Deviance	n.p.	ΔAIC_c	Weight
$m + m^2 + f + f^2 + mf$	831.1	11	3.52	0.07	548.4	11	3.10	0.09	313.2	8	3.16	0.06
$m + m^2 + f + f^2$	831.1	10	1.42	0.20	550.7	10	3.16	0.08	313.5	7	1.15	0.17
$m + m^2 + f + mf$	852.1	10	22.41	0.00	557.9	10	10.38	0.00	316.9	7	4.56	0.03
$m + f + f^2 + mf$	832.7	10	3.04	0.09	548.8	10	1.24	0.22	313.6	7	1.21	0.16
$m + m^2 + f$	854.7	9	22.94	0.00	560.4	9	10.62	0.00	317.4	6	2.77	0.07
$m + f + f^2$	832.8	9	1.07	0.24	551.4	9	1.59	0.18	314.6	6	0.00	0.30
$m + f + mf$	855.0	9	23.23	0.00	558.7	9	8.90	0.00	317.3	6	2.74	0.08
$m + m^2$	854.9	8	21.06	0.00	564.9	8	12.89	0.00	331.5	5	14.67	0.00
$f + f^2$	833.9	8	0.00	0.41	552.0	8	0.00	0.40	323.5	5	6.66	0.01
$m + f$	857.2	8	23.35	0.00	561.7	8	9.71	0.00	318.7	5	1.85	0.12
m	857.2	7	21.28	0.00	565.3	7	11.15	0.00	333.1	4	14.12	0.00
f	858.4	7	22.46	0.00	561.8	7	7.64	0.01	330.2	4	11.17	0.00
.	858.5	6	20.53	0.00	567.4	6	11.08	0.00	342.4	3	21.28	0.00

For each site, the best recapture model (Table 3) was retained. For heading explanations, see Table 3. The most parsimonious model for each site is highlighted in bold. n.p., number of estimated parameters.

**Figure 2**

Daily emigration probability as a function of fuel deposition rates (all sites) and fuel stores (Moulouya). In the diagram for Moulouya, the circles refer to fuel stores of 0, the triangles to fuel stores of 0.2, and the diamonds to fuel stores of 0.5. The estimates are from the most parsimonious model (Table 5) with corresponding SEs. The fuel deposition rates are expressed as a percentage of lean body mass.

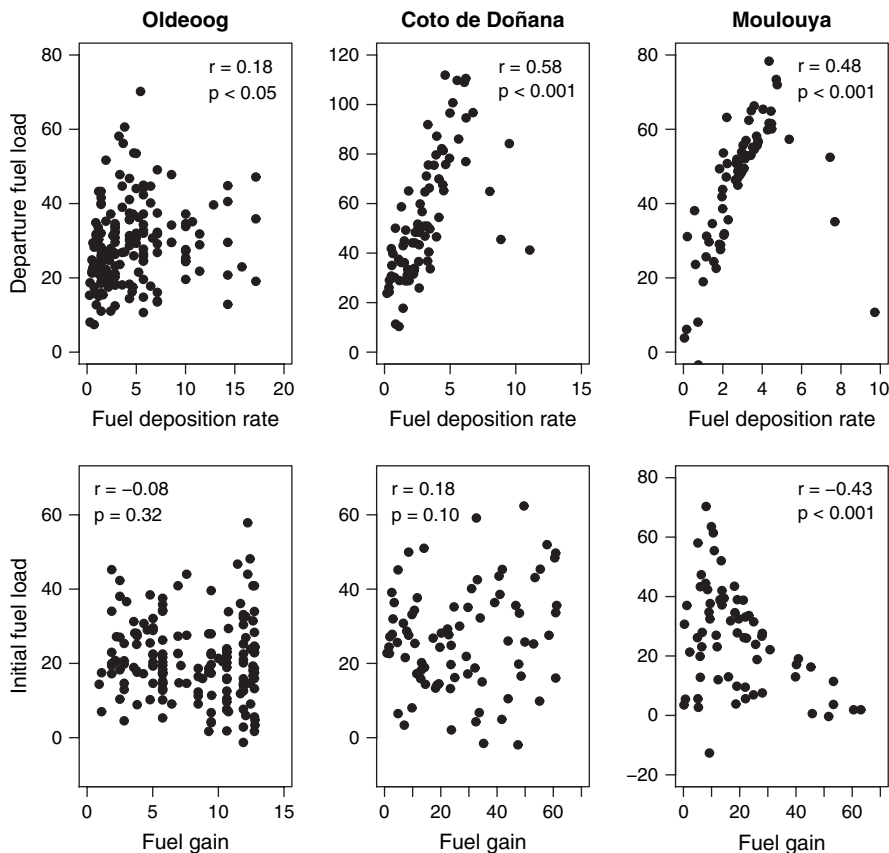
at Moulouya, but not at the 2 other stopover sites (Figure 3). At Moulouya, birds that had already high fuel stores when caught gained less fuel, whereas birds with low fuel load at capture gained a lot of fuel. This can result in an equalization of departure fuel load among birds, which was, however, not complete.

DISCUSSION

Departure of passerines from the stopover sites was primarily determined by fuel deposition rate and only secondarily by the actual energy stores. This can be concluded from the com-

bined analyses, which showed that fuel deposition rate had a stronger influence on emigration probability than energy stores at second capture at 2 sites (Table 4). In Moulouya, however, both variables were important. Yet, the effect of fuel deposition rate on emigration probability was much stronger than the effect of fuel stores over the range of observed values (Figure 3), indicating again that fuel deposition rate was more important.

The data sets available to us consisted of different species from different sites. Therefore, we cannot tell whether the observed differences between data sets are due to species or site differences. For the following reasons, we think that differences between data sets reflect differences between sites, rather

**Figure 3**

Relationship between departure fuel load and fuel deposition rate and between initial fuel load and fuel gain of passerines at 3 stopover sites. All variables are expressed as percentage of lean body mass. Given are the correlation coefficients (r) and their significance (P).

than differences between species. First, all 3 species are similar-sized passerines, winter in sub-Saharan Africa, have similar migration routes in Europe, and have basically similar migration strategies (night migrants dependent on terrestrial stopover sites). Second, it was observed repeatedly that stopover behavior varies along the migration route and with the ecological context (Jenni and Schaub 2003). Our discussion assumes therefore that differences between data sets are due to site differences and that Moulouya represents the only stopover site in front of a large ecological barrier, the Sahara desert.

Changes in body mass consist mainly of changes in fat stores and wet protein. Fat is 8.5 times more energy dense than wet protein (Jenni and Jenni-Eiermann 1998). Therefore, changes in body mass indicate changes in energy stores only if the fat and wet protein varies in parallel. This is true in most small birds investigated (Lindström and Piersma 1993).

Because fuel deposition rate appears to be an important factor determining departure, birds should be able to assess it within a short time. This is likely because the variation of fuel deposition rates from day to day at a given stopover site is rather small (Schaub and Jenni 2001b). The selection of a habitat patch that allows rapid fuel deposition (i.e., a high habitat quality patch) is essential (van Gils et al. 2005; Chernetsov 2006). If a bird succeeds to find a high-quality patch, it can accumulate fuel in a shorter time and hence increase migration speed.

The strong dependence of emigration probability on fuel deposition rate was primarily due to the high emigration probability when the birds lost body mass. This agrees with laboratory experiments, in which migratory restlessness of birds increases when food supply is reduced and body mass decreased (Biebach 1985; Gwinner et al. 1985; Yong and Moore 1993). It also agrees with field studies showing that birds losing mass are likely to move on (Rappole and Warner 1976; Biebach et al. 1986; Kuenzi et al. 1991). How far birds actually flew remains an open question and probably depends on the distribution of suitable habitat and current fuel stores. Possibly, reverse migration is one possibility to reach stopover sites that allow a positive fuel deposition rate (Sandberg et al. 1988; Åkesson et al. 1996).

Actual energy stores affected the departure decision only at Moulouya, the only site facing a large ecological barrier, that is, the Sahara desert which provides only few refueling places across 2000 km: the emigration probability increased with increasing energy stores (Figure 2). This results in a significant negative correlation between initial fuel load and fuel gain until departure (Figure 3). It indicates that the birds tended to reach a common threshold of energy stores on departure. Similar results have been found in departing red knots on spring migration at the last stopover site before reaching the very distant breeding areas (Atkinson et al. 2007). For passerines stopping in a Saharan oasis, no dependence between departure probabilities and initial fuel stores were found (Salewski and Schaub 2007), possibly because of a lack of statistical power or an intermittent migration strategy with refueling stopovers. At the 2 sites not facing a large ecological barrier (Oldeog, Coto de Doñana), departure decision was unrelated to actual fuel stores, and thus, birds did not try to achieve a common threshold of fuel stores before departure. This result supports the outcome of theoretical models, which predict that birds that have to cover a great distance without possibilities to refuel should accumulate enough fuel to reach the next stopover site after the barrier (Weber et al. 1998).

The variable effect of current fuel stores on emigration probability agrees with published information. Whereas some studies found a correlation between stopover duration and body mass (Cherry 1982; Bairlein 1985b; Biebach et al. 1986; Moore and Kerlinger 1987; Loria and Moore 1990; Dierschke and

Delingat 2001), the same or other studies found no such relationship (Safriel and Lavee 1988; Ellegren 1991; Kuenzi et al. 1991; Morris 1996; Dierschke and Delingat 2001). Published findings are difficult to compare because often stopover duration has not been measured reliably (Schaub et al. 2001), sample size was small, or the analyses did not account for fuel store changes over time. However, it appears that body mass often affects stopover duration at sites in front of an ecological barrier or in a desert oasis, that is, when it is useful to depart with a certain amount of fuel (Bairlein 1985a; Biebach et al. 1986; Atkinson et al. 2007). On the other hand, body mass is often not correlated with stopover duration when birds migrate over areas with many stopover sites (Jenni and Schaub 2003). If it is generally true that birds only consider their actual fuel stores for the departure decision at stopover sites facing large ecological barriers, they must be able to recognize that they face such a barrier. Visual cues may be used (e.g., seeing the coastline and the sea), as many birds refrain from crossing the sea when lean or during the later part of a migration bout (Sandberg et al. 1988; Bruderer and Liechti 1998). Another possible mechanism is the use of the magnetic field. Information from the magnetic field is used not only for orientation (Cochran et al. 2004; Mouritsen et al. 2004) but also for triggering fat deposition (Fransson et al. 2001).

Our results support the hypothesis that birds should minimize time spent on migration and that they should reach a threshold departure fuel load more than sufficient to cross an ecological barrier, when facing such a barrier. In contrast, the hypothesis that birds should stay the same time at a stopover site regardless of their (positive) fuel deposition rate is not supported. Few empirical tests have been conducted so far to examine whether birds are optimizing time or energy expenditure during migration. Most of them found a positive relationship between departure fuel load and fuel deposition rate, supporting the time-minimization hypothesis (Alerstam and Lindström 1990; Gudmundsson et al. 1991; Lindström and Alerstam 1992; Fransson 1998; Schmaljohann and Dierschke 2005), and only few found evidence supporting the energy minimization (e.g., Dänhardt and Lindström 2001). This agrees well with our finding that supports the time-minimization hypothesis at all sites. However, time minimization cannot be the only decision criterion for birds on migration, as it needs to be traded off against other factors such as predation risk. A certain degree of time minimization is not surprising in long-distance migrants because the period of migration is constrained by reproduction and molt in their annual cycle (Farmer and Wiens 1999), as well as by the availability of suitable food at fueling sites (van Gils et al. 2005).

The intrinsic factors related to departure were not the same at the 3 sites, although the time-minimization hypothesis is supported in all cases. Indeed, a positive relationship between departure fuel load and fuel deposition rate, which is usually taken as supporting the time-minimization hypothesis, can be observed for very different decision rules. For example, if a strong endogenous component regulates departure decision in such a way that stopover duration is very similar among birds and across sites (Schaub and Jenni 2001a; Erni et al. 2002) and completely independent of the actual fuel stores and fuel deposition rate, a positive correlation between departure fuel load and fuel deposition rate automatically appears. This is true unless there is a negative correlation between arrival fuel load and fuel deposition rate, yet this is rather unlikely (Schaub and Jenni 2001b). In summary, time minimization is certainly an important currency in long-distance migrants with their tight annual cycle, but its support (by a positive correlation between fuel deposition rate and departure fuel stores) adds little to the question what intrinsic factors determine the decision to leave a stopover site.

CONCLUSIONS

We explored the influence of fuel deposition rate and actual energy stores on the emigration probability of migrants from 3 different stopover sites. The fuel deposition rate appears to be the most important factor affecting the departure decision at all sites. Our findings also suggest that the criteria used to determine departure from a stopover site vary depending on the geographical position or ecological context. Small passerines stopping over in front of a large ecological barrier appear to base their departure decision not only on fueling rates but in addition also on actual fuel stores. In contrast, birds with many stopover sites available further on the migration route were not influenced by their actual fuel stores for the decision when to depart.

From our study and literature findings, it appears that passerine birds with many potential stopover sites available to them may use the following rules: if fuel deposition rate is negative, depart to another site (further along the migration route or by reversed migration back to sites seen on route); if fuel deposition rate is positive, decrease the duration of stay with increasing fuel deposition rate when migrating over continental area with many potential stopover sites; and if in front of an ecological barrier, look for a good stopover site and attain the threshold amount of fuel stores needed to cross the barrier.

Clearly, other factors also influence departure decision, such as weather factors (Schaub et al. 2004) and predation risk (Dierschke 2003; Schmaljohann and Dierschke 2005). It remains to be shown to what extent these factors further affect the decision to leave a stopover site. As suggested by Weber et al. (1998) and Jenni and Schaub (2003), the factors may interact and may change with time pressure.

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